Estuarine, Coastal and Shelf Science (2000) **51**, 529–541
doi:10.1006/ecss.2000.0694, available online at http://www.idealibrary.com on IDEAL®

Delivery of Winter Flounder (*Pseudopleuronectes americanus*) Larvae to Settlement Habitats in Coves Near Tidal Inlets

R. J. Chant[a], M. C. Curran[b,c], K. W. Able[b] and S. M. Glenn[a]

[a]*Institute of Marine and Coastal Sciences (IMCS), Rutgers University, New Brunswick, NJ 08903, U.S.A.*
[b]*Marine Field Station, IMCS, Rutgers University, Tuckerton, NJ 08087-2004, U.S.A.*
[c]*University of South Carolina Beaufort, Beaufort, SC 29902, U.S.A.*

Received 17 June 1999 and accepted in revised form 12 July 2000

The east coast of the United States is lined by a series of shallow inlet/bays systems that provide essential habitats for a number of important fish species. The strongest currents in these systems are typically found near the inlet where they are dominated by semidiurnal tidal motion. Beam-trawl sampling in the vicinity of Little Egg Inlet in southern New Jersey over several years indicates that the settlement of winter flounder, *Pseudopleuronectes americanus*, occurs predominantly within small coves just inside the inlet. Because of the strong tidal currents, horizontal motion of pre-settlement larvae is strongly influenced by advection. Based on hydrodynamic surveys of the region, a mechanism is suggested by which coves immediately inside of tidal inlets favour the delivery of estuarine larvae for subsequent settlement. The mechanism involves the filling of the coves with estuarine waters trapped just inside the inlet by flow separation during the flood. As a result, these observations suggest that coves near inlets may provide important settlement habitats for this estuarine species.

Keywords: lateral flow structure; flow separation; settlement habitats; winter flounder; larval supply; coves

Introduction

Much of the eastern seaboard of the United States is composed of a series of shallow bar built estuarine systems. The strongest currents in these systems are typically found near the inlets where they are dominated by semidiurnal tidal motion. Non-linearities generated by these strong currents in the presence of shallow depths and complex morphologies such as inlets, headlands and coves can distort semidiurnal motion (Aubrey & Spear, 1985) by transferring energy from the semidiurnal band to higher harmonics such as the M4 (6·21 h) and M6 (3·1 h) tides as well as to residual motion, such as that associated with tidally driven eddies (Zimmerman, 1979; Signell & Geyer, 1991). For example, alternating tidal vortices are commonly observed near inlets producing a complex but organized residual flow pattern characterized by a quadruplet eddy field. Imasato (1982) emphasizes the transient nature of tidally driven vortices, which have been shown to produce chaotic stirring (Awaji *et al.*, 1980; Awaji, 1982; Ottino, 1989; Geyer & Signell, 1990). This produces vigorous horizontal mixing and results in a potent dispersion mechanism that drives exchange between estuarine and coastal waters (Okubo, 1973; Onishi, 1986; Zimmerman, 1986; Wolanski, 1986; Wolanski *et al.*, 1988).

Many of these shallow estuarine systems provide spawning grounds and nursery habitats for a number of economically and ecologically important species (Able & Fahay, 1998). For example, adult winter flounder (*Pseudopleuronectes americanus*), typically enter shallow estuaries in the late fall for spawning in spring (Perlmutter, 1947; Bigelow & Schroeder, 1953; Saila, 1961; Phelan, 1992). As water temperatures rise in the early spring, demersal eggs are laid in the landward reaches of the estuaries (Bigelow & Schroeder, 1953; Pearcy, 1962; Crawford & Carey, 1985). Flounder remain in the larval stage for 4 to 6 weeks, depending on water temperature (Bigelow & Schroeder, 1953; Witting, 1995), at which point they settle to the bottom (Witting & Able, 1995; Witting & Able, in review; Sogard *et al.*, in review). If settlement does not occur within the estuary, larvae can be flushed out into coastal waters where they are presumably lost to the population (Pearcy, 1962; Smith *et al.*, 1975; Curran & Able, in review).

Little Egg Harbor in southern New Jersey is typical of these shallow inlet/bay systems. Current and sea

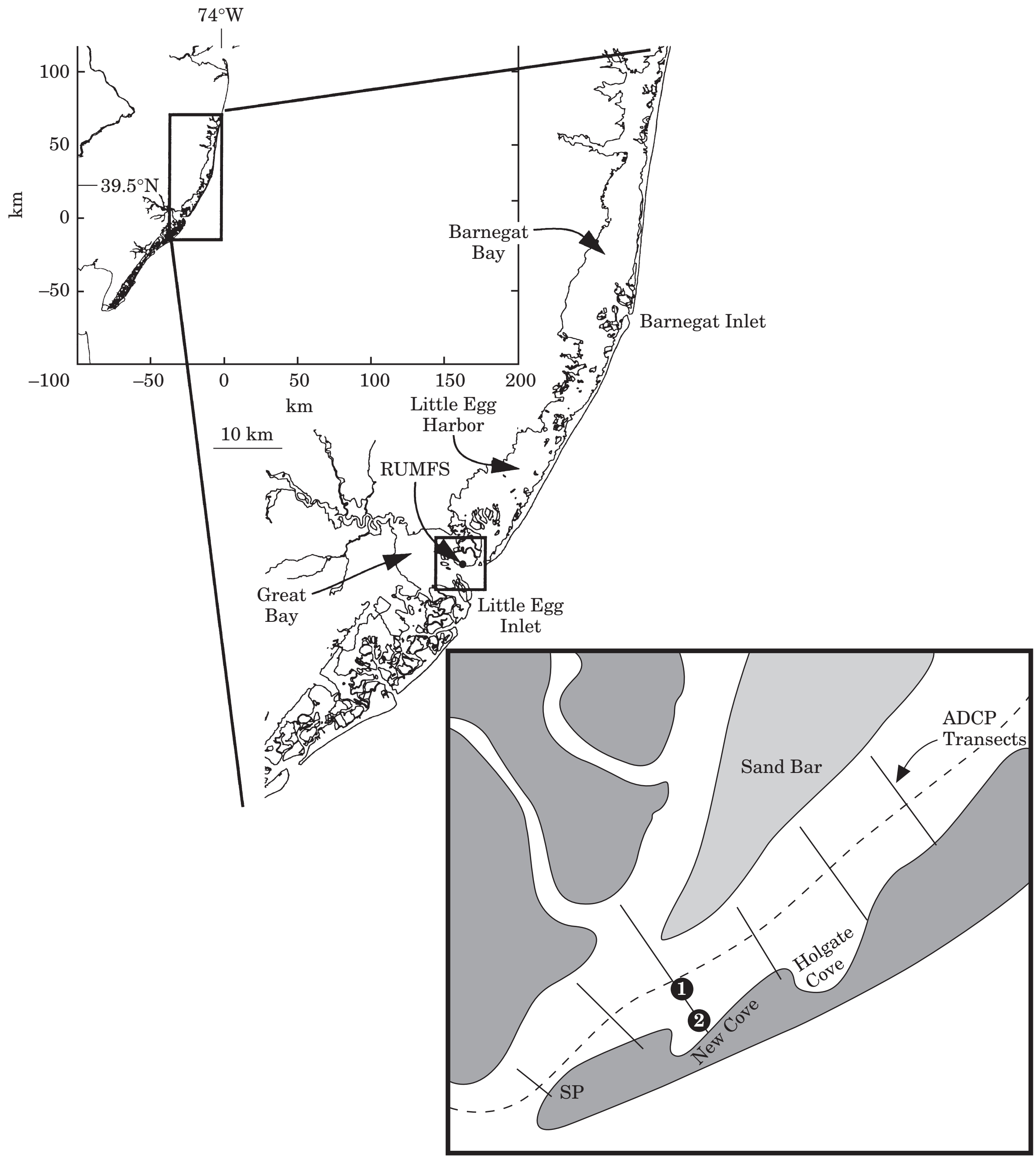

FIGURE 1. Study area in southern New Jersey, U.S.A. Intermediate map shows location of Rutgers University Marine Field Station (RUMFS). Small scale map shows location of ADCP transects (lines) and S4 deployment (black dots) in channel (1) and New Cove (2). SP refers to the point of flow separation during the flood. The channel of the intracoastal waterway is depicted by the dotted line.

level fluctuations in Little Egg Harbor are dominated by semidiurnal motion. Near the inlet the mean tidal range exceeds 1 m and tidal currents can exceed 2 m s^{-1}. Little Egg Harbor also provides spawning and nursery habitats for a number of fishery resource species, including winter flounder (Szedlmayer & Able, 1996; Able *et al.*, 1996; Able & Fahay, 1998; Jivoff & Able, in press). The larvae of winter flounder are present from mid-March through early June (Witting, 1995; Witting & Able, in review; Curran & Able, in review; Sogard *et al.*, in review) with peak abundances of 0·1–0·5 larvae m^{-3}. Settlement occurs in the shallow (<2 m) Holgate and New coves which lie just inside of Little Egg Inlet at the southern end of

Long Beach Island (Figure 1) (Witting, 1995; Witting & Able, in review; Curran & Able, in review). These prior studies indicate that juveniles settle in high densities (up to 4.1 ind m^{-2}) with peak settlement occurring approximately one week after a peak in larval densities and suggest that these cove habitats contribute to successful settlement in the system. Furthermore, these densities are among the highest reported for any flatfish species (Witting, 1995; Witting & Able, in review). After settlement is complete the mean length of the juvenile fish increases and densities diminish rapidly. The decline in densities is coincident with an increase at other regions of the estuary, suggesting that they move from the coves to other habitats (Witting & Able, in review; Curran & Able, in review).

In the spring of 1996 and 1997, we conducted a biological and physical survey in the vicinity of the cove settlement habitats. This field program was motivated by the question: why would coves in a highly dispersive and energetic region be favourable for the settlement of winter flounder larvae? In particular, do circulation patterns in the vicinity of the coves deliver late stage larvae to these coves? The biological survey measured abundance of flounder larvae on both seasonal and tidal time scales inside and outside the cove. Additionally, abundance of recently settled juveniles in the settlement habitat was monitored inside and outside the cove. Physical measurements were conducted to describe the circulation in the vicinity of the settlement habitat to describe small scale physical processes. In this paper we present the results from this interdisciplinary program and discuss the tendency for tidally transient vortices to deliver estuarine winter flounder larvae to coves immediately inside of tidal inlets.

Field programme

Hydrodynamic survey

To aid in the interpretation of the winter flounder larval distribution, hydrodynamic surveys were conducted in the spring of 1996 and 1997 in order to resolve the spatial and temporal structure of the velocity, temperature and salinity fields. The 1996 survey was conducted with a small shallow draft skiff powered by an outboard that allowed us to obtain measurements in the shallows (<2 m). The 1997 survey was conducted by the RV *Caleta*, a larger vessel that prevented us from entering some of the shallower areas covered during the 1996 survey.

A series of Acoustic Doppler Current Profiles/ Conductivity Temperature Depth (ADCP/CTD) surveys were conducted along the lines shown in Figure 1. Five surveys were conducted; one in 1996 (7 May) and four during 1997 (8, 15, 22, 29 April). The 1996 survey was conducted near spring tidal conditions, while in 1997 two spring tides (8 and 22 April) and two neap tides (15 and 29 April) were surveyed. Each survey consisted of 5–8 repeats of the series of transects shown in Figure 1 at approximately 4 knots. Each series of transects took approximately 1 h.

During low water, an exposed sand bar prevented us from sampling portions of the study area (Figure 1). This sand bar separated deeper channels on the eastern and western side of the south-eastern portion of Little Egg Harbor. A 1200 kHz BroadBand RDI ADCP was fixed with a right angle head and mounted on a Shallow Water Twin Hull (SWATH) vessel and towed abeam of the research vessel. This configuration placed the ADCP immediately below the surface and allowed us to make measurements in water deeper than 1 m in depth. Navigation utilized a differential Global Positioning System (DGPS). During the 1997 survey salinity and temperature were recorded with a SeaBird CTD.

The repeated sections provide quasi-synoptic data suitable for fixed point harmonic analysis. Harmonic analysis involved a least-squares fit of a mean plus semidiurnal and quarter diurnal signal to the fixed point data. This procedure provides estimates of synoptic flow fields throughout the tidal cycle (Geyer & Signell, 1990) which we present in this paper.

The field program also included current meter deployments. During both 1996 (23 April–9 May) and 1997 (8 April–25 May) an Interocean S4 current meter was deployed in 5 m of water in the main channel just outside the New Cove settlement habitat (Figure 1). In 1996 a second S4 was placed in 1 m (at low water) of water at the mouth of New Cove. These locations were chosen because they represent conditions in the cove and in the main channel. At both locations the S4 was placed 70 cm above the bottom. The S4 recorded horizontal current speed and direction, pressure, temperature and conductivity. The pressure record is converted to height of water above the instrument while salinity is derived from the pressure, temperature and conductivity measurements. Although bottom stress attenuates currents, these moorings do reflect hydrodynamic conditions throughout the water column because the estuary is well mixed. Wind data were collected on the meteorological tower located at the nearby Rutgers University Marine Field Station (Figure 1).

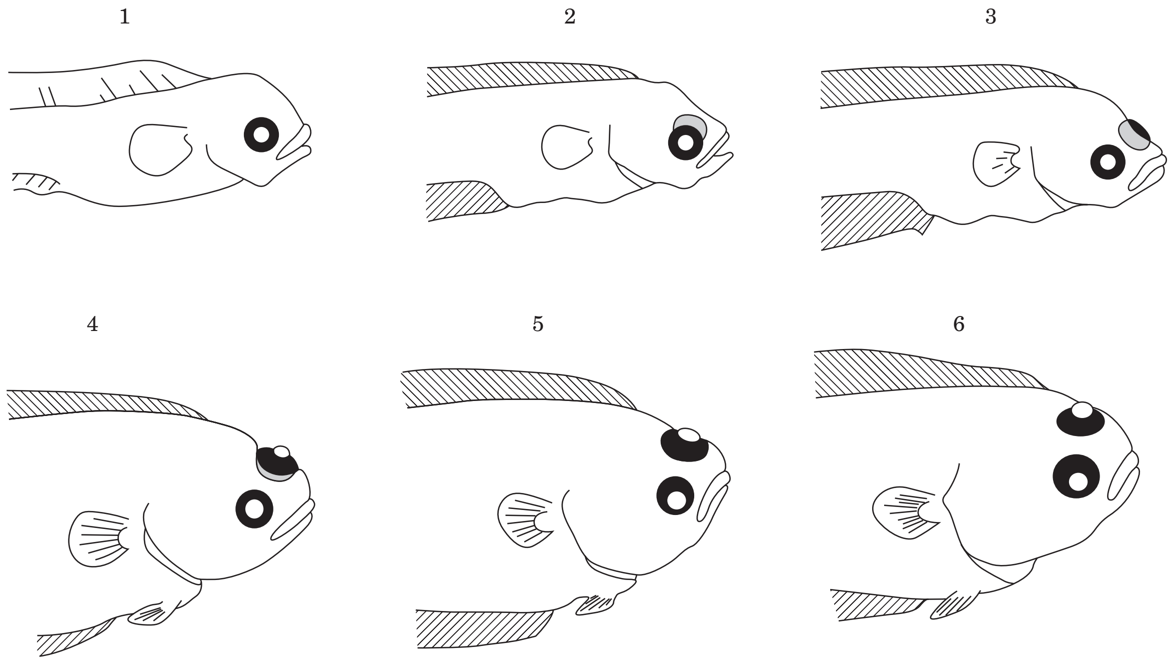

FIGURE 2. Diagrammatic depiction of morphological changes used to classify metamorphic stages of winter flounder (*Pseudopleuronectes americanus*) based on degree of eye migration. Prior to metamorphosis (premetamorph), the eyes are bilaterally symmetrical. At the first stage of metamorphosis (Stage 2) the eyes are slightly asymmetrical with the left eye just dorsal to the right eye. By Stage 3, the left eye has just reached the dorsal midline and is visible from the right side of the head. At Stage 4, the cornea is visible from the right side of the head. At Stage 5, the left eye is more than half way over the head. At Stage 6, the eyes are in the adult position. Note other developmental changes including the degree of pelvic fin development and fin ray formation. Notochord flexion begins at Stage 2 and is completed by 6.

Biological survey

In order to asses the distribution and abundance of larval winter flounder in Little Egg Harbor, a series of surface plankton net (1-m diameter, 1-mm mesh) tows (N=36 in channel, N=42 in cove) were performed weekly from 18 April–5 June 1996. We sampled at two tidal stages (maximum flooding and ebbing current) and at two sites: New Cove (<2 m in depth) and in the adjacent Intracoastal Waterway channel (6 m in depth) (Figure 1). Each sampling event consisted of three replicate tows of 3–4 min duration. A flow meter mounted in the mouth of the net was used to calculate the volume of water sampled. All samples, except two ebbing ones, were collected at night to reduce gear avoidance by the larvae. Samples were sorted immediately and the winter flounder preserved in 95% ETOH and later counted. All fish in good condition were measured to the nearest 0·1 mm notochord length (NL), and staged based on flexion state (Kendall *et al*., 1984) and eye migration stage (Figure 2). To compare differences between sites and tidal stages, we completed ANOVA procedures after square root transformation yielded a normal distribution of the data.

Beginning the week of 22 April 1996, settled individuals were collected by four replicate beam trawls (1-m, 3-mm mesh) in New Cove and immediately outside the cove during flood tide at nearly weekly intervals (N=24 in the cove, N=24 outside the cove). The beam trawl has been shown to be more efficient and less variable than other gear such as the otter trawl (Kuipers, 1975; Kuipers *et al*., 1992). A Kruskal–Wallis test for non-normal distribution of data was used to compare the beam trawl data at both sites. Both the plankton net and beam trawl have been previously evaluated to determine their reliability in sampling the early life history stages of winter flounder (Witting, 1995; Witting *et al*., 1999). At the time of sampling, surface temperature and salinity were measured with a stem thermometer and a refractometer, respectively.

Results

A comprehensive view of the hydrodynamics of the study area was constructed based on the moored and shipboard measurements which we use to interpret the space-time larval distribution patterns.

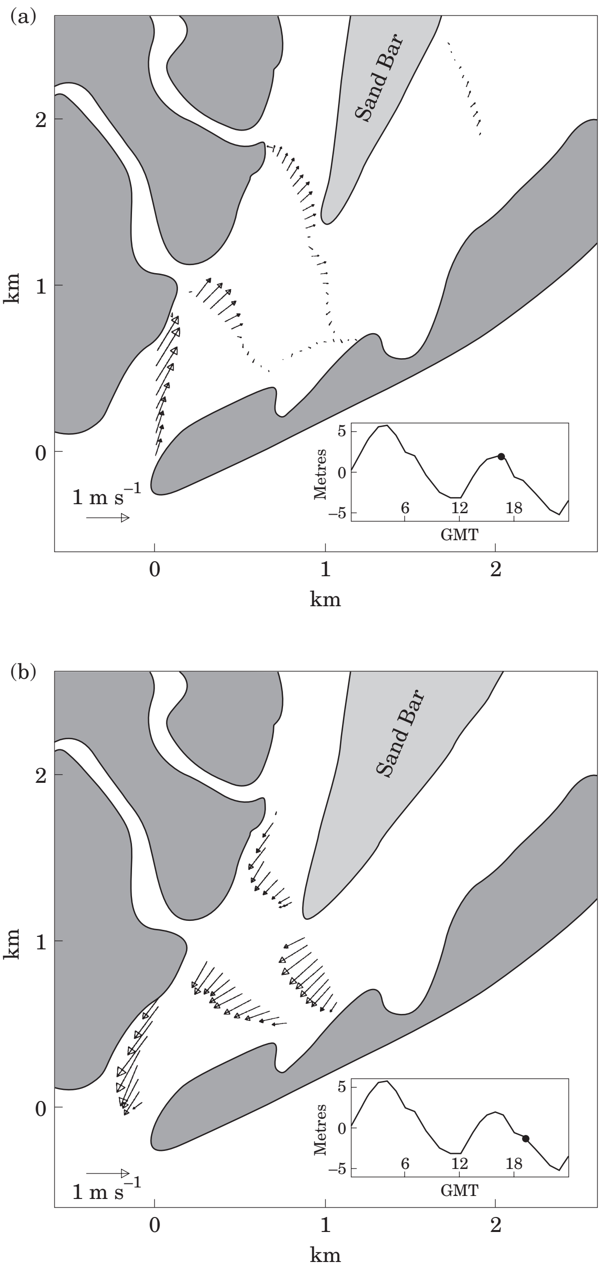

FIGURE 3. Synoptic current field during flood (a) and ebb (b) on 7 May, 1996. Sea level data are plotted in graph in lower right corner of each panel with the time of the current vector estimates. The sand bar (light grey) is more exposed during low water.

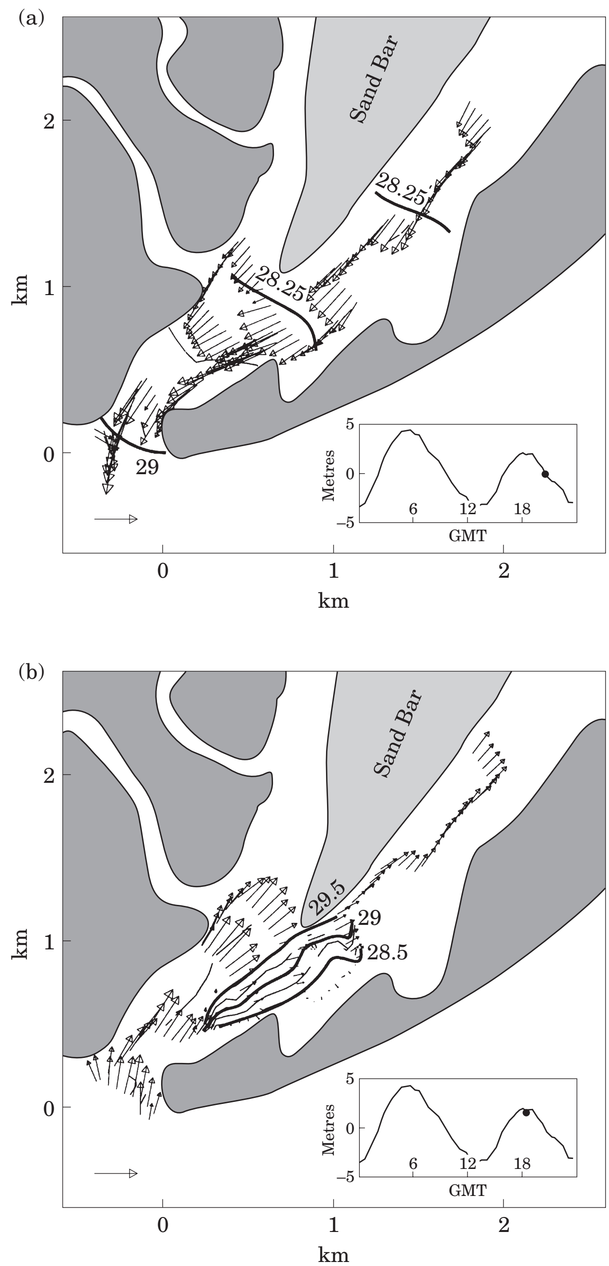

FIGURE 4. Current field and salinity during ebb (a) and flood (b) on 29 April 1997. Salinity record is contoured at 0·25 intervals. Sea-level data is plotted in graph in lower right corner of each panel with the time of the current vector field estimate denoted by the dot.

Shipboard measurements

Towed ADCP measurements obtained on 7 May 1996 emphasized appreciable lateral structure of tidal currents (Figure 3). Flooding currents were strongest on the western side of the channel, while ebbing currents are enhanced on the eastern side of the channel. The lateral structure is more pronounced during the flood because flow separation occurs nearby at the tip of the headland. For example, at high water currents on the north-western side of the channel are near maximum flood, while currents on the south-eastern side, near New and Holgate coves, are near slack.

ADCP and CTD data obtained from 29 April 1997 indicate similar tidal circulation patterns (Figure 4) as

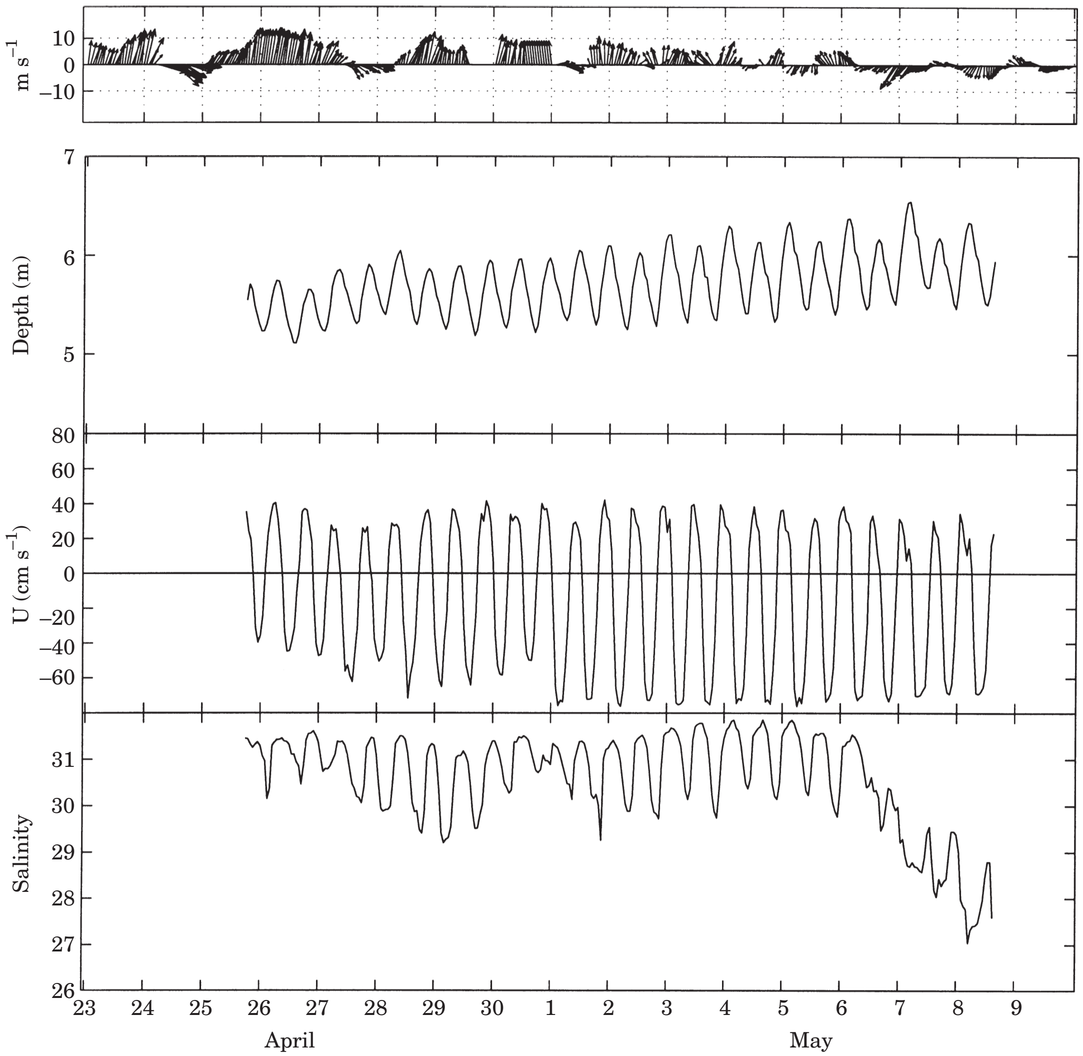

FIGURE 5. Wind and current meter data from channel S4 mooring during the 1996 field programme. Wind vectors (top panel) obtained from Rutgers University Marine Field Station's (RUMFS) meteorological tower (see Figure 1 for location). (Vectors pointing upwards represents wind blowing to the north). Pressure (second panel), along channel current speed (third panel, flooding currents are positive) and salinity record (fourth panel).

seen in 1996 (Figure 3). During ebb a weak, along-channel salinity gradient is present as estuarine waters are advected past the cove and out of the estuary. Ebb tidal currents are somewhat enhanced on the eastern side of the channel, as was the case in the 1996 survey. During this phase of the tide, sea level is dropping and the coves are emptying into the seaward flowing ebb. During the flood, currents were enhanced on the western side of the channel, while outside of New Cove and Holgate Cove currents are slack. The waters lie stagnant here because of the flow separation at the tip of the inlet. As a result, estuarine waters from the previous ebb remain outside the cove during the flood, producing the observed lateral salinity structure. Note that the salinity at the mouth of the cove during the flood is nearly the same as it is during the ebb, indicating that this fresher estuarine water was transported there on the ebb. The rising tide then pushes this estuarine water into these coves. In summary, the rising tide does not fill coves near the inlet with oceanic waters on the flood, rather they are filled with the estuarine waters trapped by the flow separation near the tip of the inlet.

1996 Mooring data

The current meter data from the channel (Figure 5) emphasize strong semidiurnal motion and indicates that at this location there is a strong seaward residual flow over the entire record. The seaward flow at

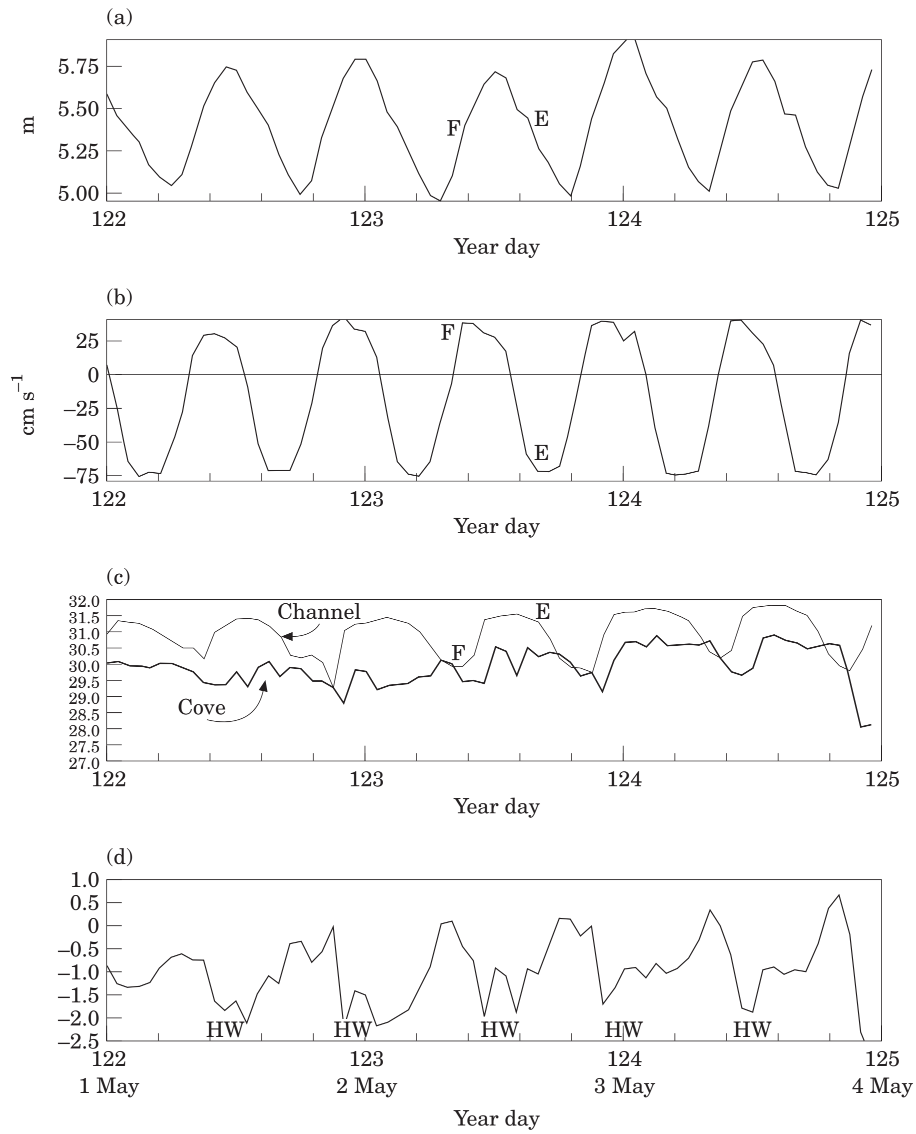

FIGURE 6. Current meter record from 2–4 May 1996. Timing of flood (F) and ebb (E) larval sampling on 2 May are denoted. Pressure (a), along channel current speed (b), salinity in cove and in channel (c) and salinity difference (d) between the mouth of New Cove and the main channel (negative values indicate fresher waters in the cove). Time of high water (HW) is denoted on last panel.

this location is due to the cross channel variability apparent in the shipboard data. Flow separation during the flood causes relatively weaker flooding currents at this mooring location and results in a mean seaward flow here. We note that the freshwater input into this system is too weak to drive two layer circulation. Salinity records exhibit semidiurnal fluctuations of approximately 2 suggesting that salinity gradients are weak. The decline in salinity commencing on 6 May is associated with a precipitation event.

Figure 6 represents a section of the 1996 S4 record during which time larval winter flounder abundances were determined in both the channel and the cove. The timing of the flood (F) and ebb (E) larval sampling is indicated on the figure. Several features of this tidal record are characteristic of shallow, well-mixed estuaries. Sea-level fluctuations are distorted by overtides. The tidal height rises faster than it drops. This tidal asymmetry is indicative of a flood dominated system. Additionally, the phasing between currents and sea level indicates that the tidal wave at this location has both progressive and standing wave characteristics (Dyer, 1997). Maximum tidal currents occur prior to high and low water while slack water occurs 1–2 h after high and low water.

The salinity time series in the channel [Figure 6(c)] shows tidal salinity fluctuations of 2.5 with maximum salinity occurring at the end of flood and minimum salinity at the end of ebb (Figure 6). Therefore salinity fluctuations lag tidal currents by approximately a quarter of the tidal cycle, or 90°. The 90° phase difference suggests that salinity fluctuations are due to horizontal advection of a salinity gradient. However, the data also suggest that the gradient is not constant. During the flood, salinities rise rapidly as oceanic waters begin flowing past the mooring, after which salinities remain fairly constant, presumably equal to the upstream oceanic salinity. A more gradual decline in salinity is evident during the ebb. This suggests that the sharp salinity gradient which advects past the mooring on the flood spreads inside the estuary before being advected past the mooring on the ebb. This is evidence of strong horizontal dispersion within the estuary.

The salinity difference between the two moorings reflects the lateral variability in salinity [Figure 6(d)]. Negative values indicate fresher conditions in the cove. Lateral salinity gradients increase rapidly during the flood and are associated with a rapid rise in salinity in the main channel, but not at the mouth of the cove. The maximum lateral salinity difference of 2 is nearly identical to the intratidal salinity variations in the channel. This suggests that estuarine waters remain in the vicinity of the cove, despite the flooding currents. In contrast lateral salinity gradients tend towards zero during the ebb.

In summary, shipboard observations emphasize enhanced lateral variability in current and salinity during the flood. In contrast, lateral structure during the ebb is weak. The lateral structure occurs during the flood because of flow separation near the tip of the inlet. This causes flooding currents to be more intense on the west side of the channel while remaining near slack on the east side of the channel, just outside the coves. The rising tide then pushes these estuarine waters into the coves. This tendency is reflected in the mooring data which emphasizes increased lateral salinity gradients during the flood. In addition, the mooring data indicates that the tidal wave near the inlet has progressive characteristics. Later we discuss the implications of this on the transport of estuarine waters into these coves.

Biological survey

Planktonic larvae were collected between 18 April through to 5 June (Figure 7) with peak larval abundances occurring in early-mid May. During the peaks, abundances exceed 130 per 1000 m^3 in the cove and

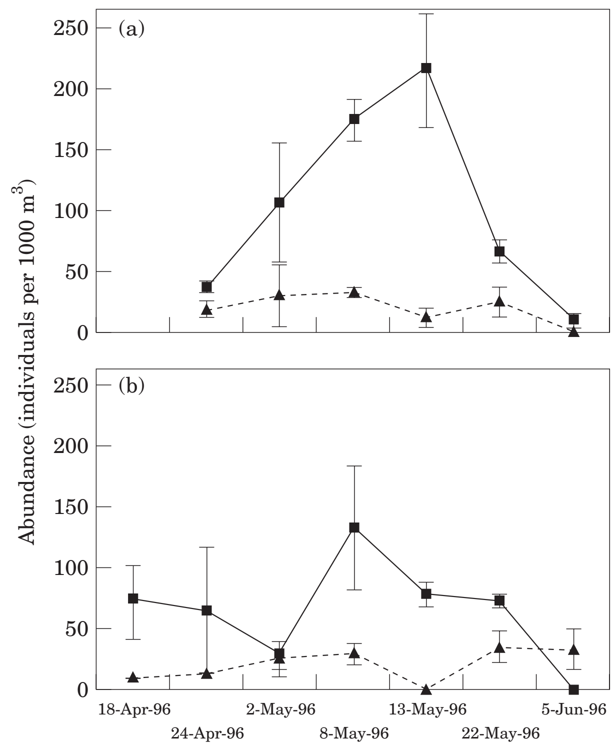

FIGURE 7. Abundance of winter flounder larvae in plankton net collections during flood and ebb tide samples in the channel (a) and cove (b). See Figure 1 for sampling locations. Error bars are ± 1 SE. Squares: flood; triangles: ebb.

200 per 1000 m^3 in the channel. On many dates, larval abundance in the cove was not quite as great as in the channel, although these results were not significantly different (P=0·2453). At both locations the lowest values were on the last sampling dates, particularly on flood tides, suggesting that most larvae had settled (Figure 7). There was a significant difference in the number of larvae collected on flood and ebb tide (P<0·001). The abundance of larvae was typically greater both in the channel and the cove during flood tide. This was most evident in the channel where abundance on the flood typically was an order of magnitude greater than during the ebb. The possible exceptions occurred at the earliest and latest collecting dates. In the cove, the differences between the flood and ebb were greater than one order of magnitude except on 2 May. There were no significant interactions between sampling site and tidal stage (P=0·1803).

The larvae in the plankton collections appear representative of metamorphizing and settling winter flounder because flexion stage individuals with migrating eyes were common (Figure 8). Recently hatched larvae (<4 mm) were not collected in either location

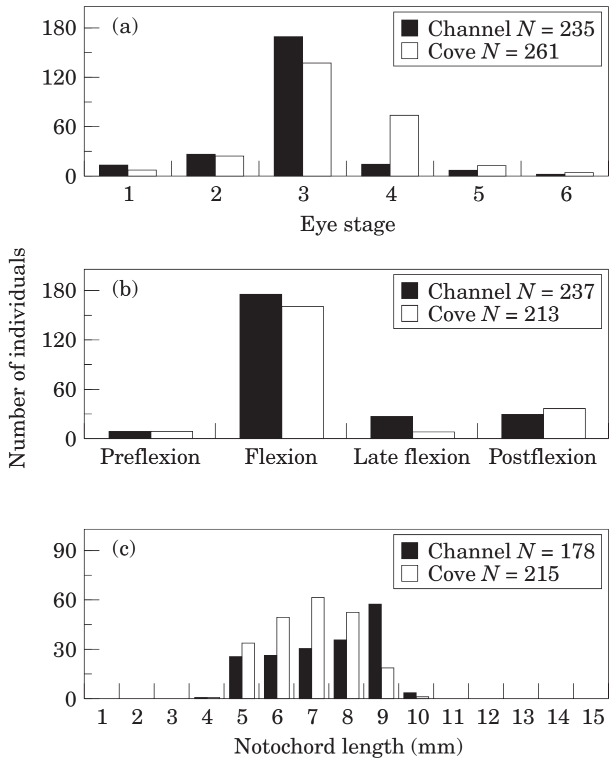

FIGURE 8. Developmental stages and sizes of larval winter flounder in channel and cove plankton net collections during 18 April–6 June, 1996; (a) eye stage; (b) notochord flexion stage, see Figure 2; (c) notochord length. See Figure 1 for sampling locations.

suggesting that hatching occurred elsewhere in the estuary. Most larvae were just beginning eye migration (stage 3), were in the flexion stage, and ranged from 5–10 mm NL. Based on chi-squared analysis, there were significant differences between channel and cove larvae with respect to the eye stage (P<0·001), flexion stage (P<0·040) and notochord length (P<0·001). For example, eye migration stages 1, 2, and 3 were slightly but consistently more abundant in the channel while stages 4, 5, and 6 were slightly, but consistently more abundant in the cove. Postflexion individuals were more abundant in the cove. As notochord length decreases during flexion, cove individuals are smaller than channel ones.

Settled juveniles were collected in the cove from 2 May through to 5 June (Figure 9). Settlement was significantly greater in the cove than outside the cove (P<0·001) with abundance in the cove exceeding 6 m^{-2} on two dates in mid-to-late May (Figure 9). Densities never exceeded 1 m^{-2} outside the cove and the peak in settlement in the cove occurred shortly after the peak larval abundance in the cove.

Discussion and conclusions

Several lines of evidence indicate that the prevailing tidal currents provide an effective means of delivery for metamorphosing winter flounder larvae into settlement areas in coves near an ocean inlet. This is supported by the consistently low numbers of settled individuals in the adjacent channel, and the fact that this occurred despite the higher abundance of pelagic larvae in the channel.

Based on this study and the findings of Witting (1995), Witting and Able (in review) and Curran and Able (in review) coves immediately inside of inlets provide settlement habitats for winter flounder. The conclusion that larvae are actively settling out in the

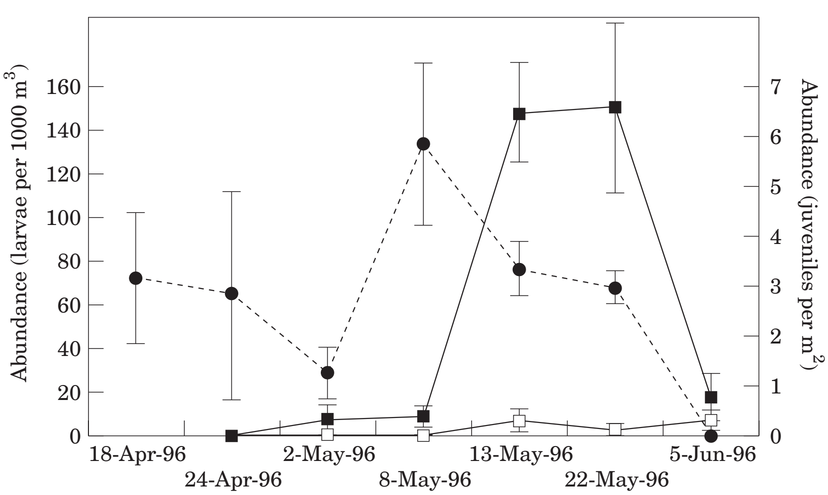

FIGURE 9. Abundance of winter flounder larvae in New Cove and settled juveniles in New Cove and outside cove during April–June 1996. See Figure 1 for sampling locations. Error bars are ± 1 SE. Filled circles: planktonic larvae; open squares: settled juveniles outside cove; closed squares: settled juveniles in cove.

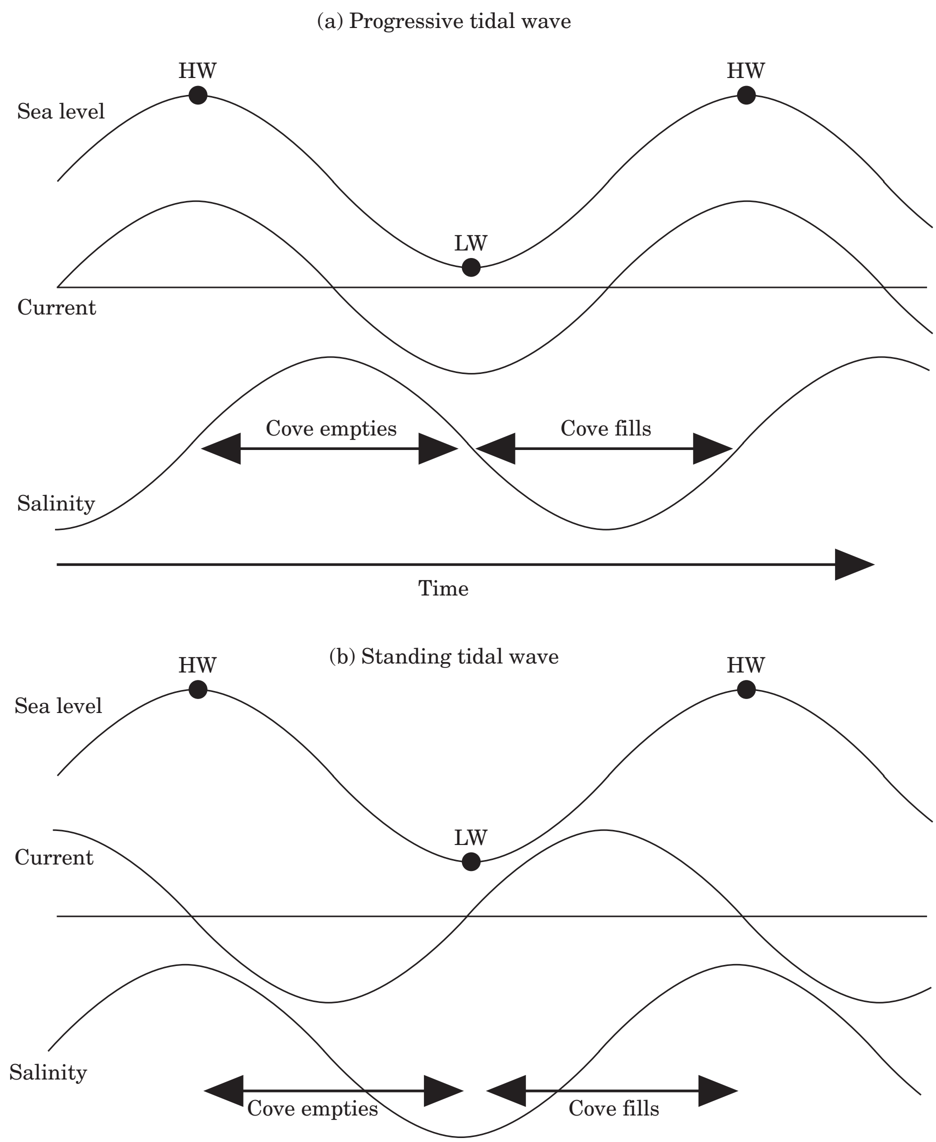

FIGURE 10. Conceptual model showing tendency for a progressive wave to fill cove with fresher estuarine waters (progressive tidal wave, a) while a standing wave fills coves with a mix of oceanic and estuarine waters (standing tidal wave, b). Salinity fluctuations are those for an advected field with a constant horizontal gradient.

cove is substantiated by the large peak in abundance of recently settled juveniles and that juvenile abundances are much greater inside the cove than immediately outside the cove or elsewhere in the estuary (Witting & Able, in review). Weak currents inside the cove may enhance settlement. In contrast, settlement may be prevented in more energetic regions, such as the adjacent channel, due to tidal period resuspensions. We suggest that the advective delivery of estuarine larvae to the cove combined with actively settling larvae could provide the mechanism that accumulates recently settled individuals within the cove.

The delivery mechanism is elucidated by the hydrographic observations, which show that these coves are preferentially filled with estuarine waters on the flood, despite their proximity to the inlet. Based on these observations we suggest two delivery mechanisms. The first mechanism is due to the progressive nature of the tidal wave. A progressive wave would deliver more estuarine waters to a cove than a standing wave. This is summarized in the schematic in Figure 10 (note that it is the tidal wave in the channel that we characterize as progressive or standing). In a progressive wave maximum currents occur at high and low water, while slack water occurs at mid-tidal stage.

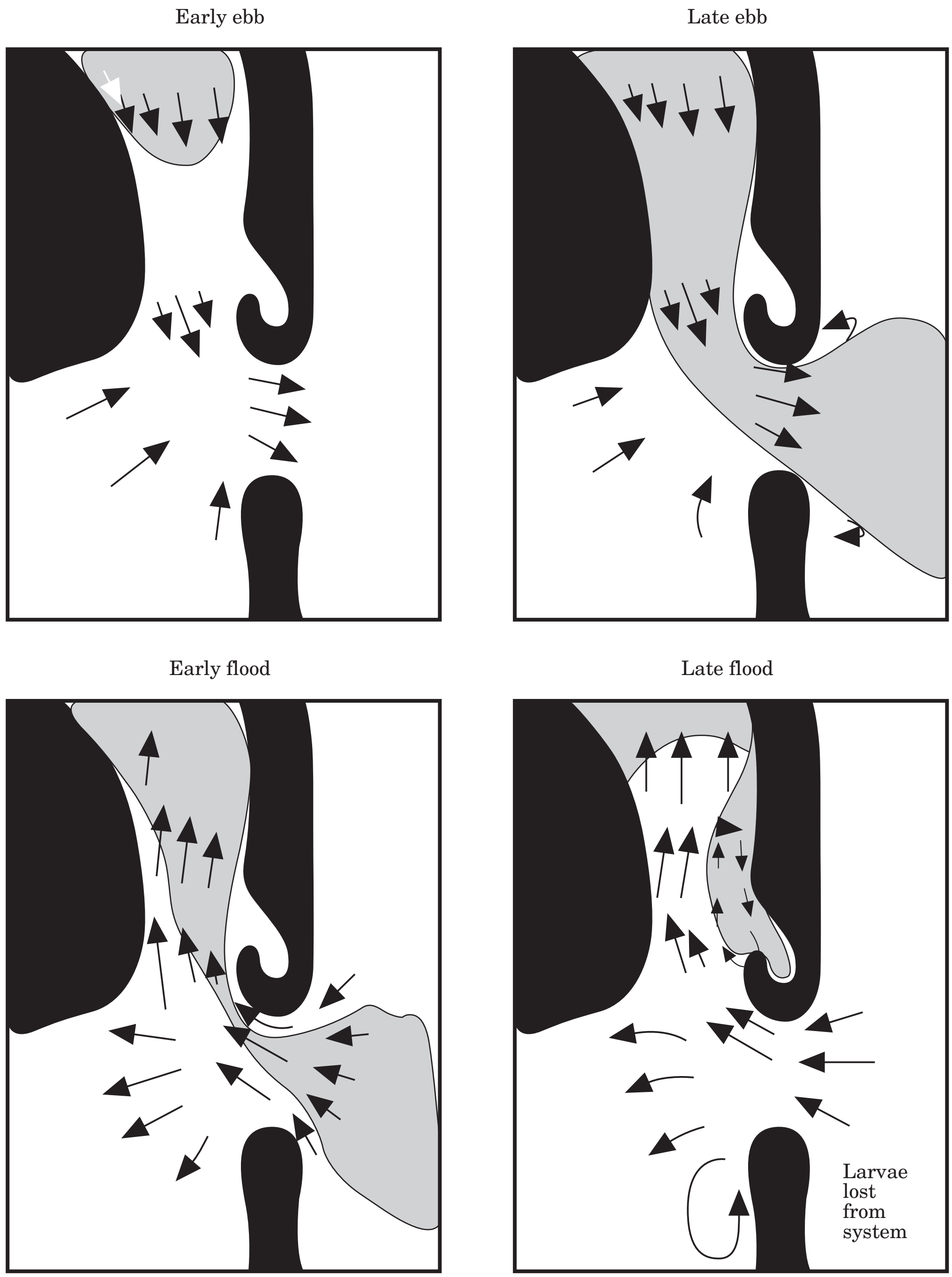

FIGURE 11. Schematic illustrating larval winter flounder delivery mechanism. Shaded areas represent estuarine water, dark areas represent land masses.

Maximum salinity occurs at the end of flood, which corresponds to the mid-tidal stage on the falling tide, while minimum salinity occurs at mid-stage during the rising tide. Consequently, as coves fill with the rising tide they are preferentially filled with fresher, estuarine waters. In contrast, in a standing wave slack water occurs at high and low tide and thus maximum and minimum salinity occurs at high and low water, respectively. As a result, these coves are filled with a mixture of oceanic and estuarine water.

The second mechanism is due to the cross-channel structure. In the case of the coves studied here, cross channel variability appears to be the dominate mechanism delivering estuarine waters to the coves immediately inside the inlet. The delivery is associated with flow separation during the flood which causes the relatively fresher waters immediately inside the inlet to lie stagnant during the flood. The cross channel structure associated with the flow separation is clearly evident in the shipboard data (Figures 3 and 4) and is apparent in the lateral salinity gradient (Figure 6), both of which show enhanced cross channel salinity gradients during the flood. As the tidal stage rises the coves fill with the trapped estuarine waters. If these waters contain larvae ready to settle, each tidal cycle brings new larvae into the cove, where weaker tidal energy favours settlement.

A conceptual model of this trapping mechanism is presented in Figure 11. This trapping may be augmented by the lack of suitable settlement habitats in the energetic main channel regions, where tidal period sediment resuspension may occur. Note that only the coves immediately inside the inlet would be filled with estuarine waters. Coves further in the estuary, upstream of where the lateral boundary layer reattaches to the shore (Batchelor, 1967; Van Dyke, 1982) would tend to be filled with oceanic waters during the flood.

At this point, we are not able to determine why larval abundances are highest during the flood. In particular, is the local time rate of change of larval abundances consistent with horizontal advection or does vertical migration play a significant role? Further, can this behaviour vary with hydrographic regime (Burke *et al.*, 1998)? Clearly, to resolve these questions, larvae need to be sampled at higher temporal and vertical resolution. Some of these issues will be addressed in our future work.

Acknowledgements

A large number of individuals from the Rutgers University Marine Field Station assisted in the collections of larvae and juvenile winter flounder. Notable among these are S. Lucas and S. Blasko. Winter flounder illustrations are courtesy of S. Blasko. Financial support was provided by the Marine Field Station and the Institute of Marine and Coastal Sciences (IMCS). Robert Chant acknowledges support from the Rutgers/NOAA Cooperative Marine Education and Research program (NA67FE0381). 9801). This publication was also supported by the National Sea Grant College Program of the U.S. Department of Commerce's National Oceanic and Atmospheric Administration under Grant # NA76-RG0091. The views expressed herein do not necessarily reflect the views of any of those organizations. NJSG-00453. This is IMCS Contribution No. 2000-16.

References

Able, K. W. & Fahay, M. P. 1998 *The First Year in the Life of Estuarine Fishes in the Middle Atlantic Bight*. Rutgers University Press, New Brunswick. 342 pp.

Able, K. W., Witting, D. A., McBride, R. S., Rountree, R. A. & Smith, K. J. 1996 Fish of polyhaline estuarine shores in Great Bay—Little Egg Harbor, New Jersey: a case study of seasonal and habitat influences. In *Estuarine Shore: Evolution, Environments and Human Alteration* (Nordstrom, K. F. & Roman, C. T., eds). John Wiley and Sons Ltd, New York, pp. 335–353.

Aubrey, D. G. & Speer, P. E. 1985 A study of non-linear tidal propagation in shallow inlet/estuarine systems. Part 1. Observations. *Estuarine, Coastal and Shelf Science* **21,** 185–205.

Awaji, T. 1982 Water mixing in a tidal current and the effect of turbulence on tidal exchange through a strait. *Journal of Physical Oceanography* **12,** 501–514.

Awaji, T., Imasato, N. & Kunishi, H. 1980 Tidal exchange through a straight: A numerical experiment using a simple model basin. *Journal of Physical Oceanography* **10,** 1499–1508.

Batchelor, G. K. 1967 *An Introduction to Fluid Dynamics*. Cambridge University Press, Cambridge, England, 615 pp.

Bigelow, H. B. & Schroeder, W. C. 1953 Fishes of the Gulf of Maine. *U.S. Fish Wildlife Service Fish Bulletin* **74,** 1–577.

Burke, J. S., Ueno, M., Tanaka, Y., Walsh, H., Maeda, T., Kinoshita, I., Seikai, T., Hoss, D. E. & Tanaka, M. 1988 The influence of environmental factors on early life history patterns of flounders. *Journal of Sea Research* **40,** 19–32.

Crawford, R. E. & Carey, C. G. 1985 Retention of winter flounder larvae within a Rhode Island salt pond. *Estuaries* **8,** 217–227.

Curran, M. C. & Able, K. W. Annual stability in use of coves near inlets as settlement areas for winter flounder (*Pseudopleuronectes americanus*). *Estuaries* (in review).

Dyer, K. 1997 *Estuaries: A Physical Introduction, 2nd edition*. John Wiley and Sons Ltd, West Sussex, England, 195 pp.

Geyer, W. R. & Signell, R. P. 1990 Measurements of tidal flow around a headland with a shipboard acoustic Doppler current profiler. *Journal of Geophysical Research* **95,** 3189–3197.

Imasato, N. 1983 What is tide-induced residual current? *Journal of Physical Oceanography* **11,** 1307–1317.

Jivoff, P. & Able, K. W. Characterization of the fish and selected decapods in Little Egg Harbor. *Journal of Coastal Research* (in press).

Kendall, A. W. Jr., Ahlstrom, E. H. & Moser, H. G. 1984 Early life history stages of fishes and their characters. In *Ontogeny and Systematics of Fishes* (Moser, H. G., Richards, W. J., Cohen, D. M., Fahay, M. P., Kendall, A. W. & Richardson, S. L., eds). Amer. Soc. Ichthyol. Herpetol. Spec. Publ. No. 1. Allen Press, Lawrence, Kansas.

Kuipers, B. R., Maccurrin, B., Miller, J. M., van Der Veer, H. W. & Witte, J. I. J. 1992 Small trawls in juvenile flatfish research: their development and efficiency. *Netherlands Journal of Sea Research* **29,** 109–117.

Kuipers, B. 1975 On the efficiencies of a two-metre beam trawl for juvenile plaice (*Pleuronectes platessa*). *Netherlands Journal of Sea Research* **9,** 69–85.

LeBlond, P. H. 1978 On tidal propagation in shallow rivers. *Journal of Geophysical Research* **83,** 4717–4721.

Okubo, A. 1973 Effect of shoreline irregularities on streamwise dispersion in estuaries and other embayments. *Netherlands Journal of Sea Research* **6,** 213–224.

Okubo, A. 1994 The role of diffusion and related physical processes in dispersal and recruitment of marine populations. In *The Biophysics of Marine Larval Dispersal (Coastal and Estuarine studies)* (Sammarco, P. W. & Heron, M. L., eds), AGU, Washington D.C. pp. 5–32.

Ohishi, S. 1986 Roles of large scale eddies in mass exchange between coastal and oceanic zones. In *Physics of Shallow Estuaries and Bays* (Lecture notes on Coastal and Estuarine Studies, vol. 16) Van de Kreeke, J., ed.). Springer-Verlag, New York, pp. 168–177.

Ottino, J. M. 1989 *The kinematics of mixing: Stretching, chaos and transport*. Cambridge University Press, Cambridge, Melbourne, Sydney, 364 pp.

Pearcy, W. G. 1962 Distribution and origin of demersal eggs within the order Pleuronectiformes. *Rapports et Proces-Verbaux des Reunions Conseil International Exploration de la Mer* **27,** 232–235.

Perlmutter, A. 1947 The mlackback flounder and its fishery in New England and New York. *Bulletin Bingham Oceanographic Collection Yale Univ.* **11,** 1–92.

Phelan, B. A. 1992 Winter flounder movements in the inner New York Bight. *Transactions of the American Fish Society* **121,** 777–784.

Saila, S. B. 1961 A study of winter founder movements. *Limnology and Oceanography* **6,** 292–298.

Signell, R. P. & Geyer, W. R. 1991 Transient eddy formation around headlands. *Journal of Geophysical Research* **96,** 2561–2575.

Signell, R. P. & Butman, B. 1992 Modeling tidal exchange and dispersion in Boston Harbor. *Journal of Geophysical Research* **97,** 15591–15606.

Smith, W. G., Sibunka, J. D. & Wells, A. 1975 Seasonal distribution of larval flatfishes (Pleuronectiformes) on the continental shelf between Cape Cod, Massachusetts, and Cape Lookout, North Carolina, 1965–1966. *NOAA Tech. Rept. NMFS SSRF-691*.

Sogard, S. M., Able, K. W. & Hagan, S. M. Long term assessment of settled and growth of juvenile winter flounder (*Pseudopleuronectes americanus*) in New Jersey estuaries. *Journal of Sea Research* (in review).

Szedlmayer, S. T. & Able, K. W. 1996 Patterns of seasonal availability and habitat use by fishes and decapod crustaceans in a southern New Jersey estuary. *Estuaries* **19,** 696–709.

Williams, G. C. 1975 Viable embryogenesis of the winter flounder, *Pseudopleuronectes americanus* from 1.8 to 15°C. *Marine Biology* **33,** 71–74.

Witting, D. A., Able, K. W. & Fahay, M. P. 1999 Larval fishes of a Middle Atlantic Bight estuary: assemblage structure and temporal stability. *Canadian Journal of Fish and Aquatic Science* **56,** 222–230.

Witting, D. A. 1995 *Settlement of winter flounder* Pleuronectes americanus, *in a southern New Jersey estuary: spatial and temporal dynamics and the effect of decapod predation*. Ph.D. Dissertation, Rutgers University, New Brunswick, New Jersey.

Witting, D. A. & Able, K. W. 1995 Predation by sevenspine bay shrimp *Cragon septumspinsosa* on winter flounder *Pleuronectes americanus* during settlement: laboratory observations. *Marine Ecology Progress Series* **123,** 23–31.

Witting, D. A. & Able, K. W. Settlement, growth and dispersal of winter flounder (*Pseudopleuronectes americanus*) in a southern New Jersey estuary. *Marine Ecology Progress Series* (in review).

Wolanski, E. 1986 Water circulation in a topographically complex environment. In *Physics of Shallow Estuaries and Bays* (Lecture notes on Coastal and Esturine Studies, vol. 16) Van de Kreeke, J., ed.). Springer-Verlag, New York, pp. 154–167.

Wolanski, E., Drew, E., Able, K. M. & O'Brien, J. 1988 Tidal jets, nutrient upwelling and their influence on the productivity of the alga *Halimeda* in the Ribbon Reefs, Great Barrier Reef. *Estuarine, Coastal and Shelf Science* **25,** 169–201.

Van Duke, M. 1982 *Album of Fluid Motion*. Parabolic Press, Stanford, California, 174 pp.

Zimmerman, J. T. F. 1979 On the Euler-Lagrange transformation and the Stokes' drift in the presence of oscillatory and residual currents. *Deep-Sea Research* **26, 226505–26520.**

Zimmerman, J. F. T. 1986 The tidal whirlpool: a review of horizontal dispersion by tidal and residual currents. *Netherlands Journal of Sea Research* **20,** 133–154.